Ecological Research (1993) **8**, 215–224

Recovery of a *Sasa tsuboiana* population after mass flowering and death

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The recovery process of a *Sasa tsuboiana* population after a mass flowering and death in 1977 was investigated by 15 years of observation in the Hira Mountains, Kinki district, western Japan. Seed production was high (6600–13 800 seeds m^{-2} in *Sasa* plots and 3900 seeds m^{-2} in a forest plot) but emergent seedling density was low (14–21 seedlings m^{-2}), probably because of seed predation by *Microtus montebelli* occurring between seed shedding and the next spring. The seedling density had decreased further by the next year and the *S. tsuboiana* population recovered from only a limited number of seedlings. In spite of such a low initial density, the *S. tsuboiana* population was able to regenerate successfully and attained the previous full stand height in 7–16 years. *Miscanthus sinensis* invaded and delayed the recovery of *S. tsuboiana* in one plot, but *S. tsuboiana* became dominant as it caught up with the height of *M. sinensis*. Seedling growth patterns, such as frequent tillering, the onset of rhizome extension in the early stage of seedling growth and frequent culm production from rhizomes, played important roles in the successful regeneration of *S. tsuboiana*.

Key words: loss of seeds; mass flowering; population recovery; *Sasa tsuboiana*; seedling growth.

INTRODUCTION

Sasa, the dwarf bamboo, is distributed widely from the temperate and the boreal zones in Japan and the adjacent areas in the Sino–Japanese floristic region (Suzuki 1978). It often forms such dense pure stands and undergrowth layers in forests that other species cannot invade the *Sasa* population.

Sasa species, like other bamboos in temperate regions, are long-living, monocarpic plants. They flower then die simultaneously in a wide area after rhizomatous vegetative reproduction during a long period, reportedly greater than 60 years (Ueda 1961; Campbell 1985). Their populations recover from even-aged seedlings after the mass flowering and death, and it takes a long time for the seedlings to grow to the full developed stage. Community components and community structure may change after the death of *Sasa* populations, because the light conditions on the ground surface are improved (Nakashizuka 1988; Makita 1992). The effects of simultaneous death on the vegetation have also been reported for other understory bamboos in temperate regions, such as *Chusquea* spp. in Chile (Veblen 1982) and *Sinarundinaria* spp. in China (Taylor & Qin 1988).

There are several hypotheses about the adaptation of the flowering habits of bamboos. For example, Janzen (1976) proposed a satiation hypothesis in which the mast fruiting habit of bamboos has been evolved to diminish the loss of seeds by predation. Simmonds (1980) asserted that synchronous monocarpy is effective in allowing seedlings to avoid the competition from their parents (the parental competition hypothesis). However fundamental documentation on the regeneration of the bamboos is too insufficient to provide support for these hypotheses. A few reports have described the demographic

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Accepted 8 March 1993.

features in the seedling population of *Sasa kurilensis* (Rupr.) Makino et Shibata (Kudoh & Ujiie 1990; Makita 1992) but no report has been published to describe the whole process from mass flowering to full recovery from the seedlings.

The present study aimed to describe the whole recovery process of a *Sasa tsuboiana* Makino population and the vegetation changes, based on 15 years of observation after a mass flowering in 1977. The objectives of this paper were: (i) to determine the seed productivity; (ii) to trace the demographic processes of the seeds and seedlings; (iii) to determine the period for recovery; and (iv) to observe the interference of other species in the recovery.

STUDY SITES AND METHODS

Sasa tsuboiana bloomed extensively in 1977 in the Hira Mountains (35°12′N; 135°53′E), Kinki district, Japan (Makita *et al.* 1988). The study area was located near Kojoro-Pass (1101 m a.s.l.) in the southern part of the Hira Mountains, where the *S. tsuboiana* grassland is widely distributed, surrounded by deciduous scrubs and forests (Murata 1977). This area has a cool temperate climate and is characterized by snowfall 0.3–1.8 m in depth (Konno 1977), from late December to late March. The structure of *S. tsuboiana* grassland in this area is influenced by wind. Wind reduces *Sasa* height and culm longevity while increasing culm density (Konno 1977). Three *Sasa* plots (S1, S2 and S3) were set up at sites of different culm height and one forest plot (F) was set up in a secondary deciduous forest with *Sasa* undergrowth to observe how the differences in population structure affect seed production and the recovery process after die-off. The three *Sasa* plots were located on a gentle slope (~18°) facing southeast. Plot F was on the northwestern slope (~22°) and was composed of *Quercus mongolica* var. *grosseserrata* (Bl.) Rehder et Wilson, *Sorbus alnifolia* (Sieb. et Zucc.) C. Koch, *Acanthopanax sciadophylloides* Fr. et Sav., *Stewartia pseudocamellia* Maxim. and others, about 10 m high.

Florets of 20 randomly sampled inflorescences in each plot were counted on 10 July 1977 to estimate the floret density. All the inflorescences in four 0.5 m × 0.5 m quadrats in each plot were collected on 11 August 1977, when most seeds had already ripened, and the numbers of inflorescences and sound seeds were counted. The sound seeds were weighed after being oven-dried at 80°C for 48 h.

Ripe seeds were shed in mid-August 1977. The number of sound seeds was counted on 21 August 1977 and 12 April 1978 to determine the loss of fallen seeds. Four 0.5 m × 0.5 m quadrats in the *Sasa* plots and eight quadrats of the same size in the forest plot were used at each sampling time. After counting the sound seeds on plants and removing culms, all the litter was gathered and four soil samples were collected with soil sampler (10.6 cm in diameter, 5.0 cm in depth) in each quadrat. The sound seeds were sieved out from the sampled litter and soil, and counted.

Ten 1 m × 1 m permanent quadrats were set up in each plot in August 1977. Coverage and the maximum height for every plant species in each quadrat were measured. Culm density of *S. tsuboiana* seedlings was also counted in each quadrat. These surveys were carried out every summer from 1977 to 1991, except in 1990. Culm density of *S. tsuboiana* in 1978 was counted on 22 October, because germination of *S. tsuboiana* had not finished by the summer census. Illuminance was measured at 9–10 points per quadrat under cloudy condiions with an illuminance meter (Pocket-lux, Lichtmesstechnic, Berlin). The illuminance at the open site was measured at the same time to calculate the relative illuminance (RI). It was measured on the ground surface in 1977, 1979, 1981, 1983 and 1986, and above the *S. tsuboiana* seedlings in 1979, 1981, 1983 and 1986. In plot F, the illuminance above the flowered culms was also measured in 1977.

Sasa tsuboiana seedlings were collected randomly in December 1978, 1979 and 1980, and April 1982 to measure seedling weight and to count the numbers of culms and branches. Early snow fall prevented sampling in 1981 and the sampling was done after snow melt in 1982. Each collected seedling was separated into leaves, culms and branches, and rhizomes after counting the number of culms and branches. Seedling density, or genet density, was estimated by the culm density, counted in the field survey, divided by the mean number of culms per collected seedling. In this paper the number of shoots refers to the sum of culms and branches. The separated organs were oven-dried at 80°C for 48 h then weighed. Individual seedlings could not be collected thereafter because the seedlings extended many rhizomes, which made it difficult to separate each seedling.

RESULTS

Seed production

Sasa tsuboiana flowered from late May to the beginning of August 1977 (Makita *et al.* 1988). Flower density varied greatly among plots depending on the structure of the population (Table 1). Inflorescence and floret densities were highest in plot S1 where culm density was highest and culm was shortest, although the number of florets per inflorescence was least. The seed density produced was also widely variable among the plots (Table 1). More seeds were produced in *Sasa* stands than in the forest plot. Among the *Sasa* stands, the taller population produced more seeds. The difference in the seed weight among plots showed the same tendency as the difference in the number of produced seeds.

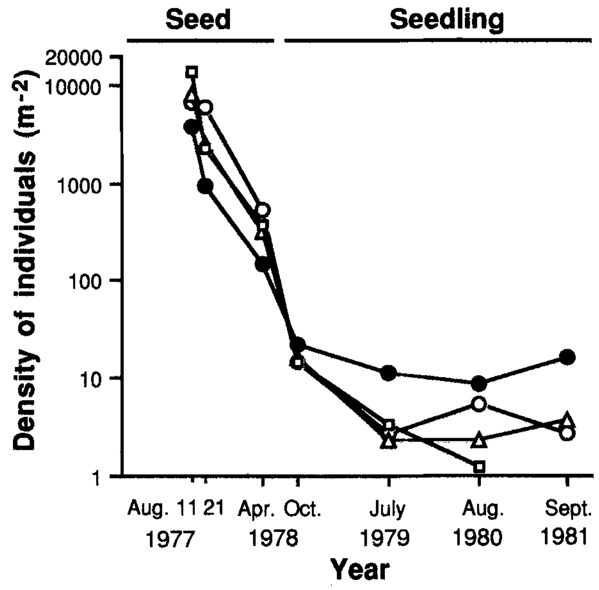

Fig. 1. Changes in individual density of *Sasa tsuboiana*. Densities on 11 August 1977 are the numbers of seeds on plants, and those on 21 August 1977 and on 14 April 1978 are the seeds on plants and in the litter and soil. (○) Plot S1; (△) plot S2; (□) plot S3; (●) plot F. No observation was made in plot S3 in 1981.

Demographic processes of the seeds and seedlings

The number of seeds decreased remarkably just after seed shedding (Fig. 1), especially in plots S2, S3 and F. The total number of seeds on maternal plants and those in the litter and soil on 21 August 1977 was only 20–30% of the produced seeds counted on 11 August 1977. The numbers of seeds in the next spring were 300–500 m^{-2} in the *Sasa* plots and 150 m^{-2} in the forest plot, which indicates that 92–97% of the produced seeds were lost before April 1978.

Seedlings of *S. tsuboiana* emerged from early summer to autumn in 1978. Emergent seedling density in October 1978 was 14–18 m^{-2} in *Sasa* plots and 21 m^{-2} in the forest plot. Seedling mortality was high during 1978–79 (75–85% in the *Sasa* plots and about 50% in Plot F) and, as a result, the *S. tsuboiana* population recovered from only a few seedlings m^{-2} in the *Sasa* plots and about ten seedlings m^{-2} in the forest plot.

Table 1 The structure of the flowered *Sasa tsuboiana* populations, and flower and seed production in each plot

	Plot			
	S1	S2	S3	F
Height (cm)	51.3 ± 2.5	90.0 ± 5.0	120.0 ± 5.0	116.0 ± 33.0
Culm density (m^{-2})	371.0 ± 102.9	171.0 ± 7.6	90.7 ± 8.3	32.0 ± 11.3
Inflorescence density (m^{-2})*	1489 ± 70	860 ± 109	664 ± 62	460 ± 118
No. of florets/inflorescence†	74.2 ± 18.6	90.3 ± 44.0	99.8 ± 60.5	105.5 ± 45.2
Floret density (m^{-2})‡	110 500	77 500	66 300	48 500
Seed density (m^{-2})*	6630 ± 1919	8218 ± 2503	13 810 ± 3055	3907 ± 1091
Seed weight (g m^{-2})	63.0	102.1	150.1	32.4
Seed setting ratio (%)§	6.0	10.6	20.8	8.0

*Mean ± SD of the sampling quadrats on 11 August 1977; †mean ± SD of the 20 randomly sampled inflorescences on 10 July 1977; ‡Number of florets per inflorescence multiplied by the inflorescence density; §seed density divided by the floret density.

Recovery of the *Sasa* population

Culm density of the seedling population slightly decreased in 1979, then showed a marked increase, before decreasing again in all plots (Fig. 2), while coverage and height showed continuous increases (Figs 3, 4). Plot S1 was different from the other plots in that the fluctuation of culm density was less remarkable (Fig. 2) and the increase in coverage was slower (Fig. 3). However, the delay in plot S1 during the early period was not observed for the height gain (Fig. 4). Seedlings of *S. tsuboiana* had exceeded the height of the original flowered population in each *Sasa* plot by 1991.

Figure 5 represents the changes in mean RI values above the *S. tsuboiana* seedlings and on the ground surface. Two factors affected the light conditions of the *Sasa* seedlings: the standing dead culms of the flowered population and the cover of vegetation higher than the *Sasa* seedlings. Flowered culms died in the year of flowering and had fallen within a few years, which resulted in the increase in the RI values measured above the *Sasa* seedlings. Nevertheless, the light conditions for *Sasa* seedlings in plot S1 were not improved, mainly because of the cover of *Miscanthus sinensis* Anderss, which showed a large, rapid increase in its coverage in plot S1, but not in the other plots (Fig. 6). It had grown more abundantly in shorter *S. tsuboiana* plots than in taller plots before the mass flowering of *S. tsuboiana* (Konno 1977). After the die-back of *S. tsuboiana* in plot S1, *M. sinensis* enlarged its coverage by the establishment and fast growth of many seedlings as well as the enlargement of the clumps established before the mass flowering. Wind dispersed seeds of *M. sinensis* were probably more abundant in plot S1 than in any other plot. Furthermore, heavy litter might prevent the early establishment of *M. sinensis* seedlings in the taller *Sasa* plots where the biomass of the *Sasa* population before flowering was much more than in the shorter population (Konno 1977).

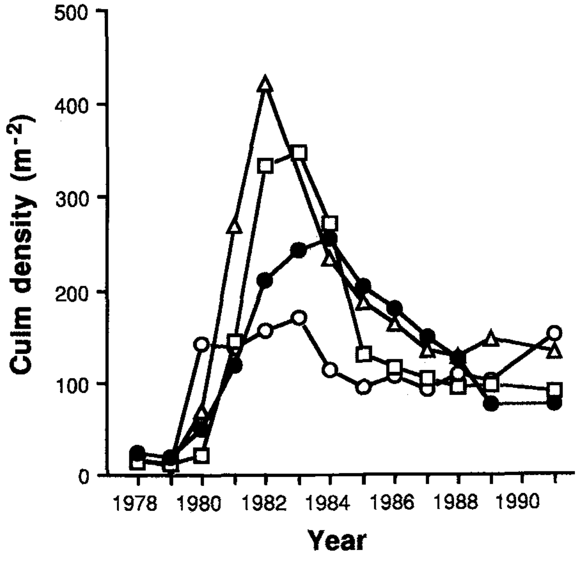

Fig. 2. Changes in the mean culm density of *Sasa tsuboiana*. Symbols are the same as in Fig. 1.

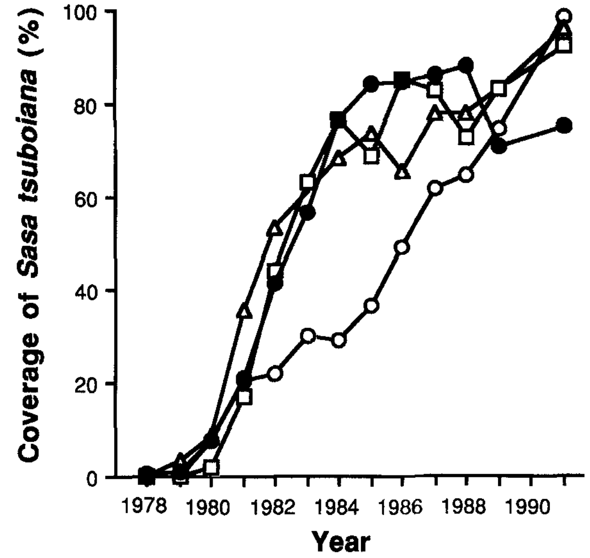

Fig. 3. Changes in the mean coverage of *Sasa tsuboiana*. Symbols are the same as in Fig. 1.

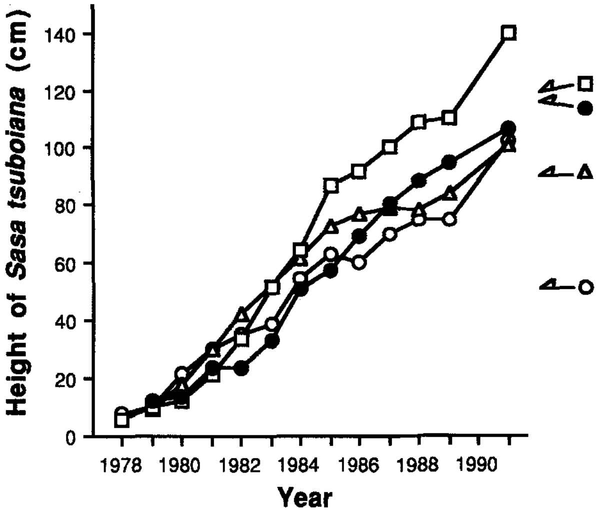

Fig. 4. Increase in the mean height of *Sasa tsuboiana*. Arrows show the heights of the flowered populations. Symbols are the same as in Fig. 1.

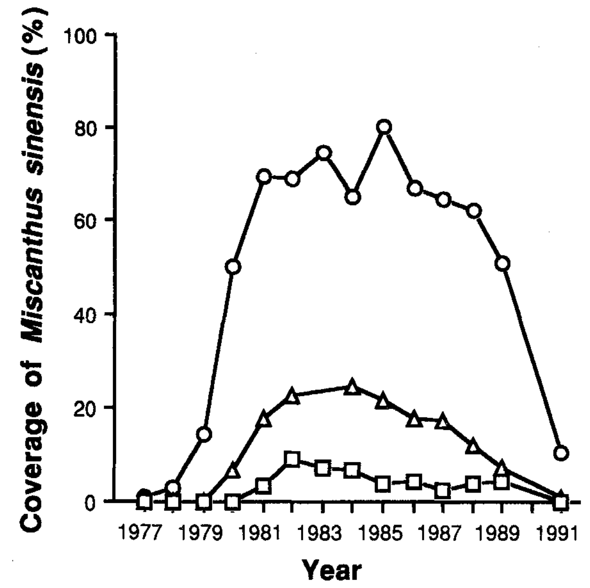

Fig. 6. Changes in the mean coverage of *Miscanthus sinensis* in *Sasa* plots. *Miscanthus sinensis* did not grow in the forest plot. Symbols are the same as in Fig. 1.

The height growth of *M. sinensis* surpassed that of *S. tsuboiana* in the early stages (Fig. 7). *Miscanthus sinensis* reached its mature height in a few years, while *S. tsuboiana* showed continuous height growth during the observation period. The coverage of *M. sinensis* decreased as the height of *S. tsuboiana* caught up with that of *M. sinensis* in plot S1 (Fig. 7).

In plots S2 and S3, *Eupatorium chinense* L. var. *simplicifolium* (Makino) Kitam. predominated temporarily in 1979–80 and shrub species such as *Tripetaleia paniculata* Sieb. et Zucc., *Clethra barbinervis* Sieb. et Zucc. and *Ilex crenata* Thunb. increased their coverage gradually. Their growth, however, did not affect the recovery of the *S. tsuboiana* population as conspicuously as *M. sinensis* did in plot S1. *Sasa tsuboiana* predominated in plot F from the early phase of regeneration, although seedlings of some tree or shrub species, such as *Acer rufinerve* Sieb. et Zucc., *Sorbus alnifolia* and *Lindera umbellata* Thunb., invaded after the death of *S. tsuboiana*. Few tree seedlings had grown

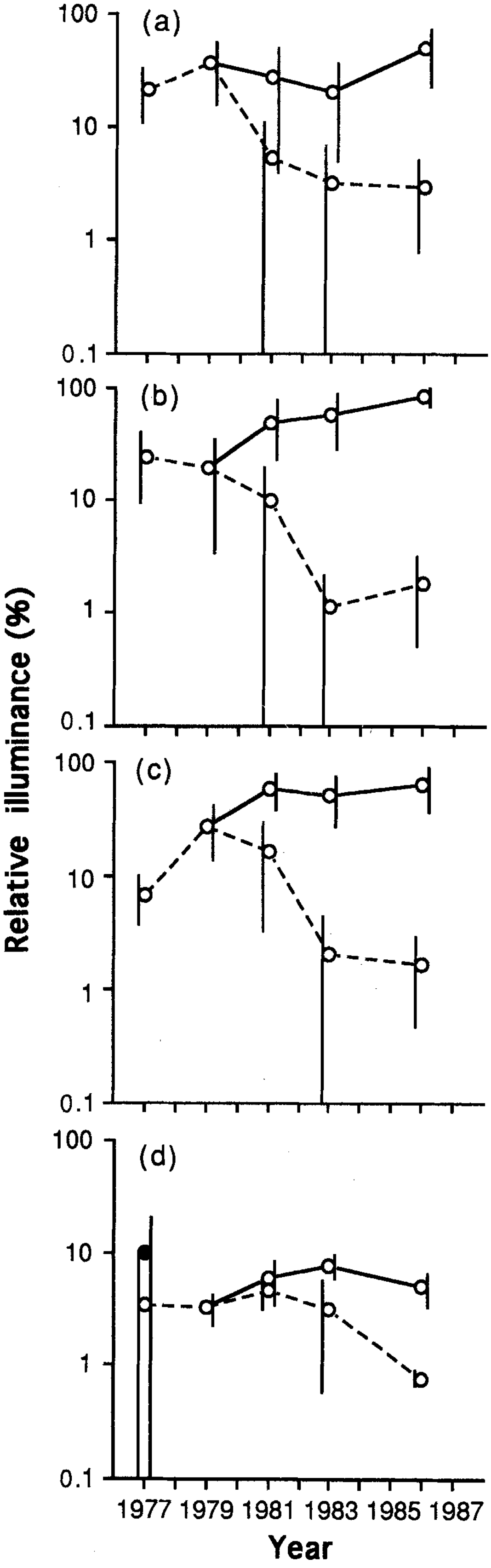

Fig. 5. Changes in relative illuminance above the *Sasa* seedling layer (——) and at the ground level (– – –) in (a) plot S1, (b) plot S2, (c) plot S3 and (d) plot F. Closed circle in (d) indicates the relative illuminance above the flowered *S. tsuboiana* culms. Vertical lines show SD.

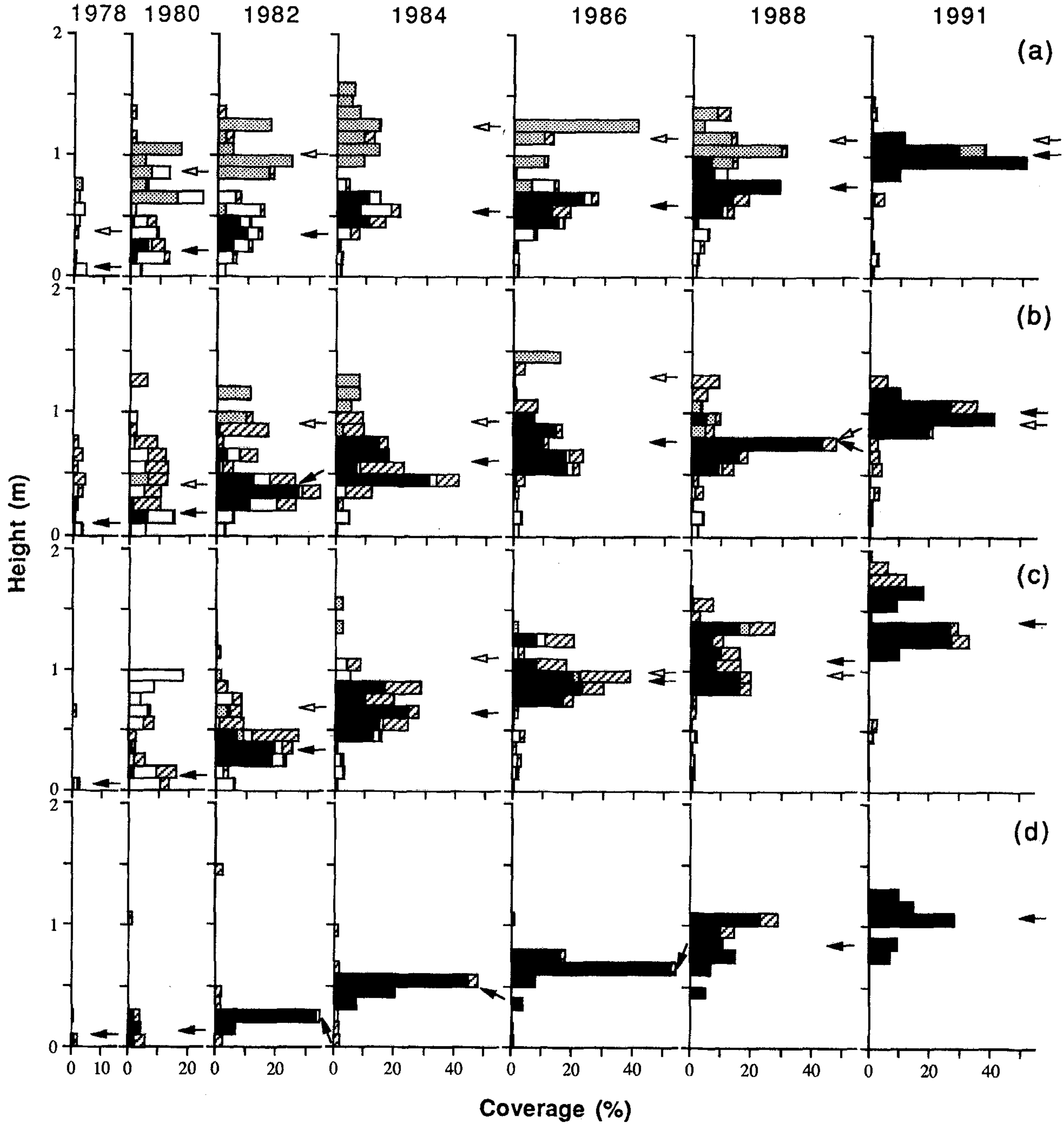

Fig. 7. Changes in mean coverage of *Sasa tsuboiana* (■), *Miscanthus sinensis* (▦), other herbs (☐) and tree species (▨) in each height class in (a) plot S1, (b) plot S2, (c) plot S3 and (d) plot F. The coverage of each species in a 1 m × 1 m quadrat was considered to be distributed only in the height class of its maximum height and mean coverage of 10 quadrats was calculated in each height class. (◄—) and (◁—) indicate the mean heights of *S. tsuboiana* and *M. sinensis*, respectively.

higher than *S. tsuboiana* under the forest canopy, in 1991.

The RI values on the ground surface decreased after 1979 in the *Sasa* plots and after 1981 in plot F. This decrease in RI was caused by the recovery of the vegetation cover.

Growth of seedlings

Sasa tsuboiana individuals produced several new culms and branches once a year in the fully developed stage. Seedlings in the early phase, however, tillered and branched several times in a growing season.

About 24% of the seedlings in plot S1 tillered even in the year of germination. The numbers of culms and shoots per seedling increased markedly as a result of frequent tillering and branching (Table 2).

Rhizome extension had been observed since 1979 in plot S2 and since 1980 in other plots (Table 2). Most seedlings in the *Sasa* plots had developed rhizomes in 1980 and about half the seedlings in plot F had developed rhizomes by 1982. The delay in the rhizome extension in plot F was due to the slower growth in the forest than in *Sasa* stands (Table 2), probably due to the low light conditions (Fig. 5). Rhizome weight was closely related with the total plant weight (Fig. 8). Some seedlings ranging from 0.1 g to 1.0 g in dry weight had rhizomes and most seedlings over 1.0 g had extended rhizomes. In plot S1 no seedlings smaller than 1.0 g had developed rhizomes, which might have been caused by underground competition with *M. sinensis*.

There is a single bud at every node of *Sasa* rhizomes and some of the buds go on to become culms. Observing the rhizome nodes before the mass flowering in the study area, Konno (1977) reported that the ratio of the nodes bearing culms was only 2–6% of the total rhizome nodes. However, 35.8, 78.3 and 52.8% of the rhizome nodes of the seedlings collected in spring 1982 bore culms or new bamboo shoots in plots S1, S2 and F, respectively. Such frequent culm production from rhizomes in the early stages of recovery was also an important factor in the rapid increase in the number of seedlings.

DISCUSSION

In spite of a high seed production (3900–13 800 seeds m^{-2}), the initial seedling density of *S. tsuboiana* was very low (14–21 m^{-2}). The number of seedlings in October 1978 was only 0.1–0.5% of the seeds produced in 1977. Mohri (1976) reported that *Sasa kurilensis* produced 9500–14 500 seeds m^{-2} and Iriguchi (1975) estimated 5000 seeds m^{-2} for *Sasa heterotricha* Koidz. Emergent seedling densities have been reported to be much lower (1–32 m^{-2}; Hokkaido Regional Forestry Office 1981; 5–20 m^{-2}, Kudoh & Ujiie 1990; 20–92 m^{-2}, Shibanuma *et al.* 1977; 1–35 m^{-2}, Yamanaka 1979) except for one case reported by Makita (1992) for *S. kurilensis* (600–800 m^{-2}). High seed production and low initial seedling

Table 2 Changes in seedling dry weight (g, mean ± SD) and the numbers of culms and shoots per plant (mean values with range in parentheses)

Plot	Year	Leaves	Culms + branches	Rhizomes	Total	No. culms/plant	No. shoots/plant	*n*
S1	1978	0.010 ± 0.011	0.021 ± 0.018	0	0.031 ± 0.029	1.3 (1–3)	1.8 (1–5)	41
	1979	0.10 ± 0.16	0.18 ± 0.32	0	0.28 ± 0.48	3.4 (1–14)	6.9 (1–35)	30
	1980	0.72 ± 0.38	1.04 ± 0.57	0.37 ± 0.31	2.13 ± 1.08	23.9 (11–42)	32.3 (16–60)	10
	1982	11.24 ± 13.20	15.96 ± 16.83	5.93 ± 11.27	33.14 ± 40.57	52.6 (4–159)	91.1 (8–282)	10
S2	1978	0.004 ± 0.003	0.012 ± 0.007	0	0.016 ± 0.010	1.0 (1–1)	1.3 (1–3)	36
	1979	0.08 ± 0.12	0.13 ± 0.20	0.007 ± 0.025	0.21 ± 0.27	4.6 (1–15)	6.7 (1–21)	40
	1980	0.85 ± 0.71	1.05 ± 0.72	0.34 ± 0.27	2.25 ± 1.65	30.0 (6–46)	40.6 (6–62)	10
	1982	11.45 ± 19.93	20.66 ± 40.35	9.07 ± 21.39	41.18 ± 81.49	72.7 (8–176)	124.4 (22–352)	10
S3	1978	0.004 ± 0.003	0.013 ± 0.007	0	0.017 ± 0.010	1.0 (1–1)	1.1 (1–2)	41
	1979	0.02 ± 0.02	0.08 ± 0.08	0	0.10 ± 0.09	3.3 (1–7)	3.6 (1–9)	31
	1980	0.48 ± 0.30	0.73 ± 0.38	0.18 ± 0.30	1.39 ± 0.92	18.5 (7–33)	25.8 (11–46)	10
F	1978	0.002 ± 0.002	0.007 ± 0.004	0	0.010 ± 0.006	1.0 (1–1)	1.03 (1–2)	30
	1979	0.02 ± 0.02	0.04 ± 0.04	0	0.06 ± 0.06	1.5 (1–4)	1.8 (1–7)	39
	1980	0.25 ± 0.16	0.28 ± 0.15	0.01 ± 0.03	0.54 ± 0.24	5.4 (3–10)	7.4 (3–13)	20
	1982	0.69 ± 0.67	1.17 ± 0.99	0.48 ± 0.70	2.34 ± 2.30	6.9 (2–19)	11.9 (2–34)	25

n = the number of collected seedlings. No observation was made in plot S3 in 1982.

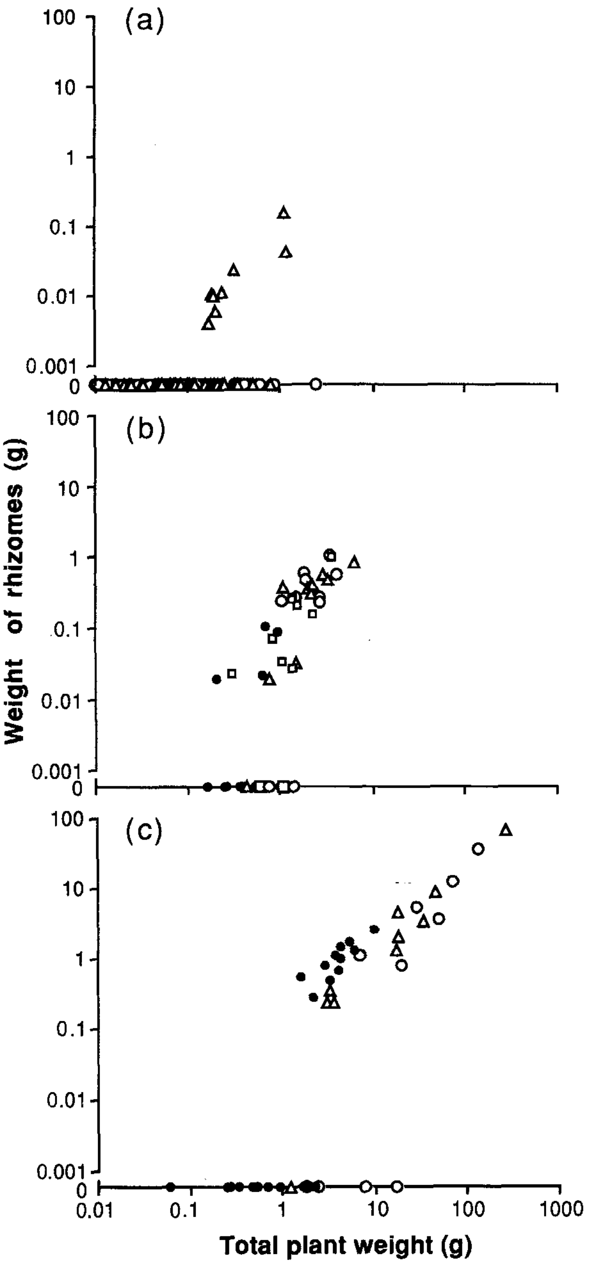

Fig. 8. Correlation between the weight of the total plant and rhizomes of *Sasa tsuboiana* in (a) 1979, (b) 1980 and (c) 1982. Symbols are the same as in Fig. 1.

density seem to be the general tendency for *Sasa* populations.

In the present study, a marked loss of fallen seeds between seed shedding and the next spring was found. Such large seed loss was presumably the main cause of the low initial seedling density. It is known that bamboo seeds are highly nutritious and that various animals eat them (Janzen 1976). The population dynamics of Murid rodents have been studied in relation to mass production of *Sasa* seeds (Mizushima 1977). Kuwahata (1979) took a census of Murid rodents near the present study plots in October 1977 and found high-density populations of *Microtus montebelli*. Many voles and their traces were also observed during the 1977 field survey in this study. It is also reported that *M. montebelli* ate many *Sasa* seeds when *Sasa* spp. fruited gregariously in Chugoku District, western Japan (Ito 1975). These observations strongly suggest that the marked reduction of fallen seeds is attributable to the predation of *M. montebelli*.

Another dwarf bamboo, *Pleioblastus argenteostriatus* f. *glaber* (Makino) Murata was reported to produce about 6000 seeds m^{-2} and to germinate at 2200 seedlings m^{-2} (Yano & Sakaguchi 1987). *Pleioblastus* spp. do not have seed dormancy, while *Sasa* seeds overwinter in a dormant state. The fact that the initial seedling density of *P. argenteostriatus* was higher than that of *Sasa* spp. presumably reflects smaller seed loss by predation because they germinate immediately after seed shedding.

Konno (1977) investigated the dry matter production of *S. tsuboiana* before flowering in the same area as the present study. According to his results, net dry matter production of the fully developed *S. tsuboiana* population is very low in the forest stand because of the low light intensity. In pure *S. tsuboiana* stands, the net production is larger in the taller populations than in the shorter ones. The difference in seed production in the reproductive phase seemed to reflect these differences in net production in the vegetative phase, because the seed production was greatest in the tallest *Sasa* plot and least in the forest plot.

Although *S. tsuboiana* could regenerate successfully in all the plots, the recovery in plot S1 was delayed by the rapid growth of *M. sinensis*. *Miscanthus sinensis* is a heliophyte that grows fast under bright conditions and forms large clumps by repeating tillering several times in a year (Kobayashi 1979). Tang *et al.* (1988) showed that the light conditions of a *M. sinensis* grassland varied widely because of the clumped patches. In the present study, the coefficient of variation of RI values above *S. tsuboiana* seedlings was greatest in plot S1. *Sasa tsuboiana* seedlings located in *M. sinensis* clumps were presumably heavily shaded but those between the patches were not. Furthermore, evergreen

S. tsuboiana could grow in the better light conditions in spring and autumn when *M. sinensis* leaves withered. Consequently, *S. tsuboiana* showed constant height growth, even in plot S1. It recovered to the height of the original flowered populations 7–14 years after flowering in the *Sasa* plots, and will be comparable to the parental population 15–16 years of the flowering in the forest plot.

The height of *S. tsuboiana* in 1991 was higher than the original flowered population, in the *Sasa* plots, especially in plot S1 where the regenerated population was 102 cm high compared to 51 cm in the parental population. Konno (1977) showed that the height of the *S. tsuboiana* population before flowering was greatly affected by the wind velocity. *Sasa tsuboiana* was shorter in areas where the wind velocity was greater. He set up a wind shelter in the low *S. tsuboiana* grassland and found that *S. tsuboiana* grew taller inside the wind shelter than outside (Konno, unpubl. data). *Miscanthus sinensis* and shrub species which enlarged their coverage after the *S. tsuboiana* died back might play a role as a wind break for *S. tsuboiana*, so that the height of the *S. tsuboiana* population might become higher than that of the parental population.

The coverage of *S. tsuboiana* increased rapidly in plots S2, S3 and F from 1980, when many seedlings began to extend rhizomes. The culm production from rhizomes was frequent at this stage. Makita (1992) made long-term observations of the regeneration process of *S. kurilensis*, where only 2–10% of 9 year old seedlings extended rhizomes. Kudoh and Ujiie (1990) also made long-term observations of the seedling cohorts of the same species and stated that culm production from rhizomes had been observed rarely during the fifteen years after germination. The onset of rhizome extension in *S. tsuboiana* was apparently earlier than in *S. kurilensis*. Features of the seedling growth pattern such as frequent tillering, early rhizome extension and frequent culm production from the rhizomes collectively contribute to the successful regeneration of *S. tsuboiana*, in spite of the low initial seedling density.

ACKNOWLEDGEMENTS

The authors are deeply indebted to Dr Eiji Suzuki, the late Dr Kazuo Naka, Dr Tohru Nakashizuka and Ms Takako Mihara for their able collaboration in the course of this study and to Dr Tatuo Kira for his suggestion that provided the initial stimulus for this study. Thanks are due to Biwako Valley Co. for providing the facilities for field work. The authors are also grateful to Dr Hideo Tabata and Dr Takashi Kohyama for their critical reading of the manuscript, to the members of the Center for Ecological Research, Kyoto University and Department of Biology, Faculty of Science, Osaka City University, for their discussion and field assistance and to the members of the Department of Biology, Faculty of Science, Nara Women's University for their field assistance.

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